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Differential effects of extreme drought on production and respiration: synthesis and modeling analysis

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Abstract

Extremes in climate may severely impact ecosystem structure and function, with both the magnitude and rate of response differing among ecosystem types and processes. We conducted a modeling analysis of the effects of extreme drought on two key ecosystem processes, production and respiration, and to provide broader context we complemented this with a synthesis of published results across multiple ecosystems. The synthesis indicated that across a broad range of biomes gross primary production (GPP) generally was more sensitive to extreme drought (defined as proportional reduction relative to average rainfall periods) than was ecosystem respiration (ER). Furthermore, this differential sensitivity between production and respiration increased as drought severity increased. The modeling analysis was designed to better understand the mechanisms underlying this pattern and focused on four grassland sites arrayed across the Great Plains, USA. Model results consistently showed that net primary productivity (NPP) was reduced more than heterotrophic respiration (Rh) by extreme drought (i.e., 67 % reduction in annual ambient rainfall) at all four study sites. The sensitivity of NPP to drought was directly attributable to rainfall amount, whereas sensitivity of Rh to drought was driven by both soil drying and a drought-induced reduction in soil carbon (C) content, a much slower process. However, differences in reductions in NPP and Rh diminished as extreme drought continued due to a gradual decline in the soil C pool leading to further reductions in Rh. We also varied the way in which drought was imposed in the modeling analysis, either as reductions in rainfall event size (ESR) or by reducing rainfall event number (REN). Modeled NPP and Rh decreased more by ESR than REN at the two relatively mesic sites but less so at the two xeric sites. Our findings suggest that responses of production and respiration differ in magnitude, occur on different timescales and are affected by different mechanisms under extreme, prolonged drought.

1 Introduction

The hydrological cycle is forecast to be intensified by climate warming, leading to increased drought frequency and severity, especially in water-limited ecosystems (IPCC, 2007). Responses of ecosystem processes to drought, especially carbon (C) fluxes, are critical given that any net change of ecosystem C balance acts as a feedback to climate change. Many studies have reported ecosystem responses to climate extremes. For example, Ciais et al. (2005) reported that heat and severe drought caused an unprecedented continental scale reduction in primary productivity with ecosystem respiration decreasing concurrently. In contrast, by analyzing observational data from a global network of eddy flux towers, Schwarm et al. (2010) found that global mean gross primary production (GPP) was more sensitive to a drought event than respiration. In a long-term field experiment, Jentsch et al. (2011) imposed an extreme drought in a constructed grassland and reported the opposite – that drought decreased soil respiration without reducing net primary production (NPP). Finally, by decreasing throughfall in a Mediterranean evergreen forest, Mission et al. (2010) reported a greater reduction in GPP than that in ecosystem respiration (ER), especially soil respiration. Such divergent responses of ecosystem productivity and respiration to extreme drought suggests that greater mechanistic understanding is needed with regard to how these two key C cycling processes are likely to respond to climate extremes.

Drought can affect production and respiration through both common and unique mechanisms. Drought lowers plant C uptake by reducing stomatal conductance and leaf area, and by increasing soil water deficit (Bréda et al., 2006), whereas soil water deficits and reduced substrate availability can reduce ecosystem respiration (Luo and Zhou, 2006). Although there are now many studies that have reported C cycling responses to both natural and experimentally imposed droughts in a variety of biomes (e.g., Reichstein et al., 2002; Ciais et al., 2005; Schwalm et al., 2012), these have not been synthesized to determine if there are any general patterns of production and respiration responses to extreme drought across terrestrial biomes. Identifying such patterns is key for determining if general mechanisms underlie production and respiration responses.

One critical limitation to both observational and experimental studies is that they are all conducted at short time scales – from seasonal to annual in length – whereas ecological responses to drought over the longer term are likely to be more complex (Anderson et al., 2011). This is especially true for heterotrophic respiration, which is affected by drought induced reductions in the soil C pool as a function of lower GPP (Mission et al., 2010). Knowing how ecosystems respond to long-term, extreme drought is important given that climate models predict an increase in the frequency and magnitude of these events in the future (Dai, 2011). We hypothesized that although the sensitivity of production and respiration to drought may differ initially, they will eventually become equivalent as carbon cycle processes equilibrate over time (Luo and Weng, 2011). Such long-term response patterns of ecosystems to drought are difficult to reveal in experiments or observational studies but can be explored by ecosystem modeling (Luo et al., 2011).

Drought has often been manipulated in global change experiments by reducing each rainfall event amount (Yahdjian and Sala, 2006; Mission et al., 2010; Cherwin and Knapp, 2012). However, as climate models have predicted decreases in rainfall frequency in the future, drought could also occur due to declines in rainfall event number (e.g., Báez et al., 2013). These two different types of drought may affect ecosystem functions differently. For example, Harper et al. (2005) observed more drought-induced reduction on aboveground NPP (ANPP) and soil CO_2 flux under natural drought caused by reducing rainfall event number and size than simply altering the size of each rainfall event. This drought-event size interaction has also been observed in shortgrass steppe where experimental droughts only reduced ANPP when rainfall events were frequent and small rather than few but large (Cherwin and Knapp, 2012).

Our objectives were 2-fold. First, we determined if general patterns of drought effects on production and respiration exist across multiple biomes based on published papers of both observational and experimental studies. Second, we used an ecosystem model to examine mechanisms possibly underlying differential sensitivity of production and respiration in four different grassland types over a rainfall gradient in Central US Great Plains. In the modeling analysis, we assessed responses of NPP and heterotrophic respiration (Rh) to a long-term severe drought imposed by either reducing the size or the number of individual rainfall events. In addition to assessing responses over longer time scales and mechanistically, we also compared responses in these sites to identical treatments, thus overcoming a weakness of syntheses of published studies that each impose drought in different ways and of different magnitudes and measure responses uniquely (Luo et al., 2011).

2 Materials and methods

2.1 Synthesis methods and data analysis

We searched ISI's Web of Science using these search strings: "(drought OR severe drought OR extreme drought) AND (ecosystem fluxes OR ecosystem carbon balance)", "drought AND NEE AND eddy covariance", "(precipitation OR drought OR rainfall) AND net ecosystem exchange AND manipulation" and "drought AND NPP AND respiration" to identify both observational and manipulative studies of drought effects on ecosystem C fluxes over global terrestrial biomes. We also used "rain forest AND eddy flux AND drought" to search for studies focused more appropriately on seasonal droughts in rain forest dry seasons. We reviewed the most relevant studies in which GPP and ER were reported in both drought and normal years or dry and wet seasons for rain forest (Table 3 and Supplement Table S1).

Drought was categorized as extreme drought when ecosystems experienced more than a 40 % decrease in annual rainfall relative to the long term average, as moderate drought with less than a 40 % but more than a 25 % rainfall decrease, and minor drought with less than 25 % rainfall reduction. The drought sensitivity of production as estimated by GPP and respiration estimated by ER for each study site was calculated as the drought induced absolute reduction relative to the normal year divided by GPP or ER in the normal years (i.e. $\Delta GPP\% = (GPP_{normal} - GPP_{drought})/GPP_{normal}$ or $\Delta ER\% = (ER_{normal} - ER_{drought})/ER_{normal}$). The significance between ΔGPP% and ΔER% was tested using paired *t* test. Seasonal drought effects on ΔGPP% and ΔER% in rainforest were not included in this analysis because of different responses and underlying mechanisms. Thus, seasonal drought effects in rainforest are discussed separately in this study.

2.2 Modeling analyses

2.2.1 Model description

The terrestrial ecosystem model (TECO) is a process-based ecosystem model and was designed to examine ecosystem responses to climatic perturbations including elevated CO_2, warming and altered precipitation (Luo et al., 2008; Weng and Luo, 2008). The algorithms applied in TECO are described in detail by Weng and Luo (2008). Here we provide a brief description, focusing on mechanisms related to drought.

TECO is composed of four major sub-models that represent canopy processes, plant growth, C transfer, and soil water dynamics. The canopy photosynthesis-transpiration submodel is a two-leaf model with multiple canopy layers, derived primarily from Wang and Leuning (1998), to simulate canopy energy balance, canopy photosynthesis and conductance. For each layer, foliage is divided into sunlit and shaded leaves. Leaf photosynthesis and transpiration are estimated by coupling the Farquhar photosynthesis (Farquhar et al., 1980) and Ball–Berry stomata-conductance model (Ball et al., 1987). In the plant growth submodel, allocation of photosynthetic assimilates depends on growth rate of leaves, stems and roots following ALPHAPHA model (Denison and Loomis, 1989), and varies with phenology following CTEM (Arora and Boer, 2005). Phenology is represented by seasonal variation in leaf area index (LAI). Leaf onset is determined by growing degree days and leaf senescence is induced by low temperature and low soil water content. The C transfer submodel simulates movement of

C from plant to soil C pools in three layers through litterfall and the decomposition of litter and soil organic C. Carbon fluxes from litter and soil carbon pools are based on residence time of each C pool and C pool sizes (Luo and Reynolds, 1999).

The soil water dynamics submodel has ten soil layers and simulates the dynamics of soil water content based on precipitation, evaporation, transpiration and runoff. Evaporation is determined by water content of the first soil layer and evaporative demand of the atmosphere. Transpiration is regulated by stomatal conductance and soil water content of layers where roots are present. When precipitation exceeds water recharge to soil water holding capacity, runoff occurs. In this study, a soil moisture scalar, ϖ, is the most important parameter because the reduction in precipitation directly affects soil water content and thus the soil moisture scalar. In TECO, relative soil water content is defined as $\varpi = (W_{\mathrm{soil}} - W_{\mathrm{min}})/(W_{\mathrm{max}} - W_{\mathrm{min}})$ where W_{max} is soil water holding capacity, W_{min} is the permanent wilting point and W_{soil} is soil water content. Photosynthesis and plant growth rate are reduced whenever ϖ is less than 0.3.

2.2.2 Study sites

The sites selected for the modeling analysis are the Konza Prairie Biological Station (Konza), the Hays Agricultural Research Center (Hays), the High Plains Grasslands Research Center (Cheyenne), and the Sevilleta National Wildlife Refuge (Sevilleta). The four grasslands are distributed along mean annual temperature (MAT) and mean annual precipitation (MAP) gradients (Table 1). Cheyenne has the lowest mean annual temperature among the four sites (Table 1). Sevilleta has much coarser soil texture than the other three grasslands.

2.2.3 Model validation

The TECO model was driven by meteorological data from eddy flux towers for Konza tallgrass prairie and Sevilleta desert grassland and from meteorological stations for the Hays and Cheyenne mixed-grass prairie sites. Meteorological data include hourly solar radiation, air temperature, soil temperature, precipitation and relative humidity from 2007–2010. For Hays, meteorological data in 2006 were used, instead of 2007 due to its incomplete record. The model was validated against daily net ecosystem CO_2 exchange (NEE) from eddy flux towers during 2007–2010 at Konza and Sevilleta (Fig. 1), along with biometric data including ANPP and soil respiration measured at these grasslands (Table 2). For all the variables, the modeled results were in good agreement with observational data (Fig. 1 and Table 2).

2.2.4 Modeling scenarios

The objective of this experimental simulation was to use the long-term records of rainfall to model extreme drought effects on ecosystem C dynamics. Therefore, the long-term records of daily rainfall data were collected from weather stations closest to each grassland. The periods of rainfall data were 1982–2010 for Konza, 1949–2010 for Hays and Sevilleta and 1949–2011 for Cheyenne. The four meteorological variables (solar radiation, air temperature, soil temperature, and relative humidity) used to drive the model were from year 2007 for Konza, Cheyenne, and Sevilleta, and from year 2006 for Hays, repeated for each rainfall year. In order to simulate the effects of extreme drought, the annual rainfall amount was reduced to 33 % of ambient rainfall by two approaches. One was to reduce each rainfall event size (ESR) by 67 % of ambient rainfall (AMB), and the other was to reduce rainfall event number (REN) to achieve the same 67 % reduction in annual rainfall as ESR. The REN treatment resulted in intermittent periods with no rain events and thus increased precipitation variability compared with ESR treatment. These two treatments allowed us to explore the differential effects of drought and increased rainfall variability on ecosystem C dynamics in different grassland ecosystems along the MAT and MAP gradients.

2.2.5 Statistical analysis

The linear regressions were conducted in SigmaPlot version 12. A student's *t* test for the slope difference between ambient condition and rainfall reduction treatments was conducted in SAS software (SAS Institute Inc., Cary, NC, USA).

3 Results

3.1 Differential drought effects on production and respiration and mechanisms: literature synthesis

We synthesized results from 39 studies that included grasslands, deciduous broadleaf forests, evergreen needle-leaf forests, woody savanna and shrubland (Supplement Table S1). Eleven out of the 39 study sites experienced extreme drought (i.e., > 40 % below long-term average rainfall), 10 sites experienced moderate drought and 18 sites were subject to minor drought. GPP was more sensitive to drought than ER under extreme and moderate drought (Fig. 2). Minor drought had no differential impacts on GPP or ER.

For the five study sites with data available, seasonal drought in rainforest had only a limited impact on GPP (Table 3) likely because the tree root systems had access to an adequate water supply in deep soil layers. Respiration, especially heterotrophic respiration was reduced due to drying of the surface soil. As a consequence, ecosystem carbon uptake actually increased under seasonal drought in tropical rainforests.

3.2 Modeled drought effect on ecosystem C variables

Both extreme drought treatments decreased annual NPP, heterotrophic respiration (Rh), NEE and soil C content with similar patterns over modeled years in each of the four grasslands (Fig. 3 and Supplement Fig. S1). The relative reduction in NPP was consistently greater than in Rh in all the grassland sites, but the difference diminished over time due to continued decreases in Rh with drought (Fig. 3a–h). Annual GPP and ER showed similar drought responses to annual NPP and Rh, respectively (Supplement Fig. S2). However, in order to reveal directional change in Rh, we used annual NPP and Rh in the model analysis. The differential responses of NPP and Rh to drought caused NEE to increase (more ecosystem CO_2 release), but the drought-induced change in NEE decreased over time (Fig. 3i–l). Drought-induced reduction in soil C content also increased over time, the same as Rh in all the study sites (Fig. 3m–p).

Annual NPP, Rh, NEE and soil C content responded differently to the two different drought types (Fig. S1 and Fig. 3). In the tallgrass prairie and the Hays mixed-grass prairie, annual NPP, Rh, and soil C content decreased more under ESR than under REN, whereas annual NPP, Rh, and soil C content decreased less under ESR than under REN in the Cheyenne mixed-grass prairie and the desert grassland (Sevilleta). Differential responses of NEE to the two drought types were contingent upon year. Overall, Sevilleta had the greatest inter-annual variability (23 %, 19 %, and 29 % average coefficient of variation over the two rainfall treatments) whereas the mixed grass site near Cheyenne had the lowest inter-annual variability (10 %, 12 %, and 17 % average coefficient of variation over the two rainfall treatments) for relative reductions in NPP, Rh, and soil C, respectively with drought.

3.3 Controls on annul C fluxes and the long-term impacts of drought

Annual NPP increased with increasing rainfall amounts for all the grasslands under each of the three rainfall scenarios (ambient, ESR and REN) (Fig. 4a–d). The slopes of change in NPP were greater under the drought scenarios than that under ambient conditions (Supplement Table S2). Annual NEE decreased with rainfall (Fig. 4i–l). The slopes were negative and smaller under drought treatments than under ambient condition (Supplement Table S2). Annual Rh was not related to rainfall under drought scenarios, but a positive linear relationship with rainfall was noted under ambient conditions for all grasslands (Fig. 4e–h). The interannual variation in the relative reduction in NPP negatively correlated with annual rainfall amount in all grassland sites except for Cheyenne (Fig. 5) and the relative reduction in Rh was positively correlated with drought-induced relative reductions in soil C content (Fig. 6).

4 Discussion

Our synthesis and modeling analysis both revealed that production (GPP and NPP) was more sensitive to moderate to severe drought than respiration (ER and Rh) and that this difference in sensitivity increased as drought became more extreme. In the modeling analysis, NPP was reduced more than Rh by extreme drought. However, the difference between NPP and Rh (i.e., NEE) diminished over time with drought over multiple years. Our findings suggest that responses of production and respiration to drought differ in magnitude, occur on different timescales and are affected by different mechanisms under extreme, prolonged drought. Additionally, the finding of different responses to drought types indicates the diverse interactive effects on ecosystem functions between rainfall variability and rainfall amount.

4.1 General patterns of drought effects on production and respiration

In the literature synthesis, GPP and ER responded differently to extreme and moderate drought, but not to minor drought, which suggests that moderate to extreme drought may override other confounding factors, for example site characteristics, climate conditions, and dominant plant species. However, during minor drought, evidence indicates that the responses of GPP and ER were largely regulated by topographic position and soil texture (Kljun et al., 2006), drought-associated high summer radiation (Granier et al., 2007) and high summer temperature (Welp et al., 2007), along with a lagged effect from previous soil water condition (Welp et al., 2007). A broad range of ecosystems were included in the synthesis (Supplement Table S1), for example grasslands, deciduous broad-leaf forests, evergreen needle-leaf forests, woody savanna and shrubland.

Thus, the general pattern of such differential responses is representative and robust across biomes.

In contrast to the general pattern, however, in rainforest ecosystems where dry seasons occur annually, seasonal drought had limited effects on GPP due to adequate water supply from deep soil layers and hydraulic redistribution by deep roots. Therefore, rainforest GPP is generally controlled more by factors such as solar radiation (Bonal et al., 2008) rather than precipitation. Indeed, previous modeling studies that included deep water supply and hydraulic redistribution closely captured the seasonal drought effects in rain forest (Baker et al., 2008). Even though trees in other ecosystems were also able to tap deep soil water (e.g., Kerhoulas et al., 2013), GPP was still reduced due to drought-increased vapor pressure deficit which causes leaf stomata to partially close (Kolb et al., 2013).

4.2 Mechanisms underlying differential response of production and respiration to drought

In agreement with the synthesis results, the modeling analysis revealed the general pattern that production (GPP and NPP) was more drought sensitive than respiration (ER and Rh). The underlying mechanisms were explored in the model analysis of four grasslands over a rainfall gradient ranging from 240 to 860 mm. The greater sensitivity of modeled NPP to extreme drought that we observed (Fig. 3) at all four sites was due to different controls of the two ecosystem C variables. In grassland ecosystems, production generally increases linearly or asymptotically with rainfall amount (e.g., Fig. 4; Sala et al., 1988; Huxman et al., 2004). Therefore, in the extreme drought treatments NPP declined almost linearly with precipitation amount. However, heterotrophic respiration, which is the mineralization of soil C, is a soil C pool-controlled ecological process that is often regulated by soil temperature over the long term in addition to soil water content and substrate availability in the short term (Luo and Zhou, 2006; Vargas et al., 2010). Soil C content is more or less stable to short-term climate variability, therefore the response of soil C to drought requires longer time periods (Fig. 3m–p and Luo et al., 2011) compared to plant physiological processes such as photosynthesis. As a consequence, Rh was less impacted than NPP in the short-term.

The model analysis also showed that the reduction in Rh increased during long-term drought due to diminishment of soil C pool size. The decrease in the soil C pool could be caused by drought-reduced NPP, the primary source of soil C. To our knowledge, we are not aware of any empirical studies that reported long-term effects of drought on soil C and Rh. However, space-for-time studies provide indirect evidence regarding ecosystem C dynamics under long-term climatic changes (Luo et al., 2011). For example, soil C declined linearly with decreasing precipitation in observations along precipitation gradients (Anderson et al., 2011; Talmon et al., 2011), which indirectly supports model results indicating a long-term drought-induced decrease in soil C content. This long-term decline in soil C content could cause the difference between the drought sensitivities of production and respiration to diminish gradually over time. Due to these differential responses over longer timescales, our modeling results showed that grassland ecosystems all released CO_2 to the atmosphere during drought, but the amount of released CO_2 decreased over time as soil C pools declined. The model results, however, would benefit from long-term field experiments to provide direct support for these results. This exploration of ecosystem sensitivity dynamics over the long term is critical for global change studies because many ecological responses are strongly regulated by slow processes (Luo et al., 2011).

Our model results also showed that Sevilleta and Cheyenne had the largest and least inter-annual variation, respectively, in the relative reduction of NPP and Rh. Soil texture has long been known to affect plant productivity through the inverse soil texture effect (Noy-Meir, 1973) and has the potential to interact with rainfall regimes to mediate the impacts of drought (Weng and Luo, 2008). The much larger inter-annual variability in relative reduction in NPP and Rh in Sevilleta could be explained by coarse-textured soils because lower average water availability can amplify drought effects (Paruelo et al., 1999). The low variability and lack of correlation between rainfall and relative reduction in NPP at Cheyenne may have occurred because the lower average temperatures for this site relative to the other three (Table 1) resulted in less evaporation, and thus increased available water for plants and constrained the inter-annual variation in sensitivity to drought. These results emphasize the need for multi-site long-term drought experiments, because inter-annual variation in precipitation as well as lagged effects from soil water storage likely play important roles in regulating ecosystem responses to climate extremes (Granier et al., 2007).

4.3 Drought attributes and differential responses of production and respiration

In our modeling analyses, total annual rainfall in the two rainfall treatments was the same. Drought imposed by reducing every event (ESR treatment) was characterized by lower rainfall event size (1/3 of ambient rainfall), but ambient rainfall frequency. In comparison, the REN treatment was characterized by ambient rainfall event size but lower frequency, and longer dry intervals between rain events. Responses of NPP and Rh to these treatments were contingent on grassland type, with greater reductions in NPP and Rh when drought was caused by every rain event becoming smaller (ESR scenario) at the two most mesic and productive grasslands (Konza and Hays) However, REN also caused in reduction in both NPP and Rh. Knapp et al. (2002) also observed that lower frequency in rainfall events without changing total rainfall in a mesic tallgrass prairie resulted in less production than ambient rainfall frequency. However, if annual precipitation amount was low (1/3 of ambient rainfall in our study), the larger rainfall event size under REN relative to ESR could lead to higher soil water content and consequently higher production (Supplement Fig. S1a and b) in mesic grasslands. More water was stored in deep soil layers under ambient rainfall event size compared to lower rainfall event size in ESR, which decreased evaporative loss to the atmosphere and increased water availability to plants. Lower rainfall frequency (i.e. REN treatment), however, led to lower NPP in xeric grasslands (Supplement Fig. S1c and d). Frequent small rainfall events (the ESR treatment) can potentially alleviate chronic water stress, whereas the longer dry period under REN inhibited early leaf and root development and consequently decreased production. Responses of Rh to the two drought types are consistent with those of NPP, indicating NPP controls the responses of Rh to different drought types.

4.4 Implications for future experimental studies

Our findings have several important implications for field experiments. First, reported observations and manipulative climate change studies are often short term. The snapshot of observed responses, therefore, may not be representative of long-term response, especially when slow ecological processes are involved. Second, many manipulated drought experiments only decrease event sizes. Our results showed that reduced rainfall event number had differential effects on ecological processes than simply decreasing the size of each rain event. Future experiments should impose drought through different patterns of rainfall size, frequency and intensity. Third, other components of ecosystem C processes should be assessed in global change experiments in addition to production. Different ecosystem C variables are likely to have different response patterns to imposed perturbation. In order to provide information on positive or negative feedbacks of terrestrial biomes to climate change, measurements of both production and respiration are needed. Fourth, macro-scale global change experiments should be carried out to capture cross-scale interactions and differential sensitivities of ecosystem types to climate change (Fraser et al., 2013).

In this ecosystem model, we did not incorporate vegetation changes under long-term climate change. Although global climate change largely affects ecosystem structure and function, it is reasonable to expect that vegetation may acclimate, adapt or change in composition as climate conditions change over time (Smith et al., 2009). For example, Isbell et al. (2013) found that production decreased following a decade of chronic nitrogen addition as a consequence of change in plant community composition. However, the responses of ecosystem variables to extreme climatic changes are unlikely to be overridden by biotic adaptation (Anderson et al., 2011). Rather, the extent of the responses might be attenuated or exacerbated (Smith, 2011). Nonetheless, further research is needed to incorporate vegetation change into ecosystem models to improve ecological forecasting.

Supplementary material related to this article is available online at http://www.biogeosciences-discuss.net/10/16043/2013/ bgd-10-16043-2013-supplement.pdf.

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Yang, F. L. and Zhou, G. S.: Sensitivity of temperate desert steppe carbon exchange to seasonal droughts and precipitation variations in Inner Mongolia, China, Plos One, 8, e55418 doi:10.1371/journal.pone.0055418, 2013.

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Table 1. Key climate, plant, and soil characteristics of four grassland ecosystem types located within the US America Great Plains.

	Konza	Hays	Cheyenne	Sevilleta
Latitude	39°05′ N	38°53′ N	41°11′ N	34°20′ N
Longitude	96°35′ W	99°23′ W	104°54′ W	106°43′ W
Grassland Type	Tallgrass	Southern mixed-grass	Northern mixed-grass	Desert/shortgrass
MAT (°C)	12.9	12.0	7.6	13.3
MAP (mm)	860	577	384	242
Soil Texture	Silty Clay Loam[1]	Silty Clay Loam[1]	Fine-loamy[2]	Sandy Loam[3]

[1] Heislter-White et al. (2009).
[2] Carrillo et al. (2011).
[3] Muldavin et al. (2008).

Table 2. Comparisons between modeled and measured aboveground net primary production (ANPP) and soil respiration (Rs).

	ANPP ($g\,m^{-2}$)		Monsoon Rs ($g\,C\,m^{-2}$)	
	Observed	Modeled	Observed	Modeled
Konza	461 (134)[a]	488 (38)	–	–
Hays	300 (–)[b]	342 (46)	–	–
Cheyenne	130 (25)[c]	163 (15)	–	–
Sevilleta	140 (3)[d]	165 (2)	63 (3)[e]	81 (8)

[a] mean ANPP from 1984–1998 (Knapp et al., 2006).
[b] Long term mean ANPP (Heisler-White et al., 2009).
[c] PHACE measurement (Personal communication).
[d] average in 2007 and 2008 (Thomey et al., 2011).
[e] average in 2007 and 2008 (Vargas et al., 2012).
Values in the parentheses are standard errors across years.
"–" mean that values were not available.

Table 3. Synthesis of published studies in differential responses of GPP and ER to extreme seasonal drought in tropical rainforest.

Site	Biome type	Results	Mechanisms	Reference	Note
Tapajos km83, Brazil	Amazonian rain forest	Seasonal drought did not impact GPP, but decreased ER	Deep rooting depth buffered drought stress on GPP	Saleska et al., 2003; Goulden et al., 2004	Eddy flux
Tapajos km67, Brazil	Amazonian rain forest	Seasonal drought reduced GPP less than ER	Adequate water supply for photosynthesis during dry season	Hutyra et al., 2007	Eddy flux
French Guiana, South America	Neotropical rainforest	Seasonal drought increased GPP, but reduced ER	Drought-associated higher incident radiation increased GPP	Bonal et al., 2008	Eddy flux
Sardinilla, Panama	Plantation	Seasonal drought reduced both GPP and ER by similar amount	Deep rooting depth buffered drought stress on GPP	Wolf et al., 2011	Eddy flux
Xishuangbanna, China	Tropical rain forest	Seasonal drought reduced less on GPP than on ER	Deep rooting depth alleviated drought stress on GPP	Zhang et al., 2010	Eddy flux

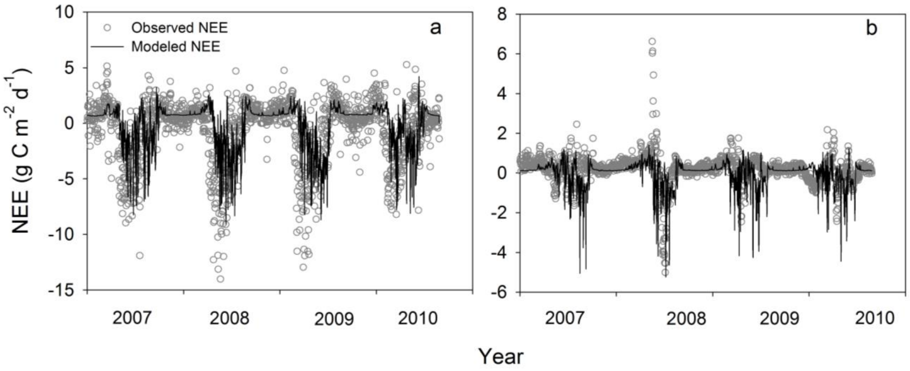

Fig. 1. Comparisons between observed daily net ecosystem CO_2 exchange (NEE) from eddy flux data and modeled daily NEE in Konza tallgrass prairie and Sevilleta desert grassland from 2007 to 2010. Open black circles represent observed daily NEE. Black solid lines represent modeled daily NEE.

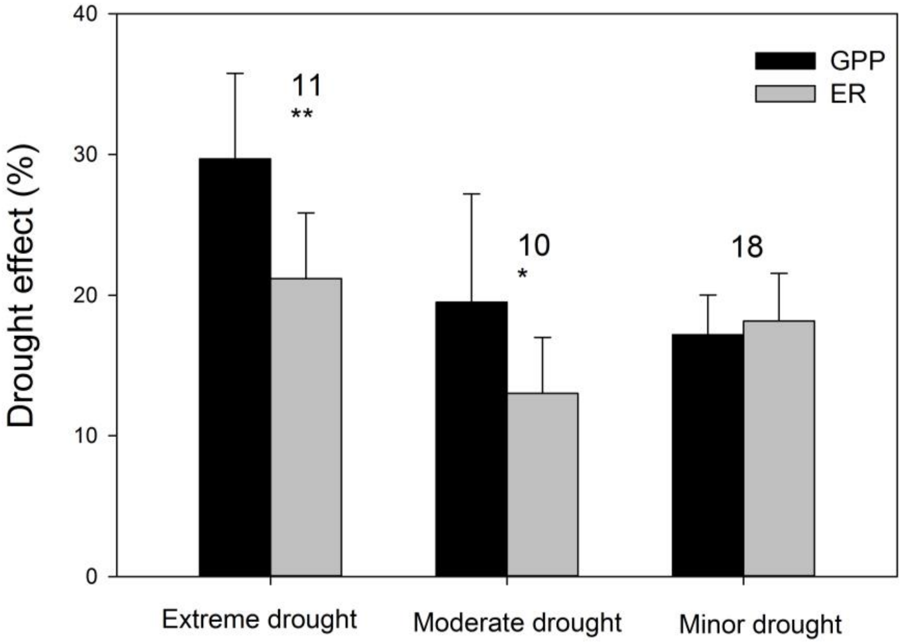

Fig. 2. Synthesized published observational and experimental results on sensitivity of gross primary production (GPP) and ecosystem respiration (ER) to extreme drought, moderate drought and minor drought. Numbers represent the number of studies included, ** represents significant ($P < 0.05$) difference and * represents marginally significant difference.

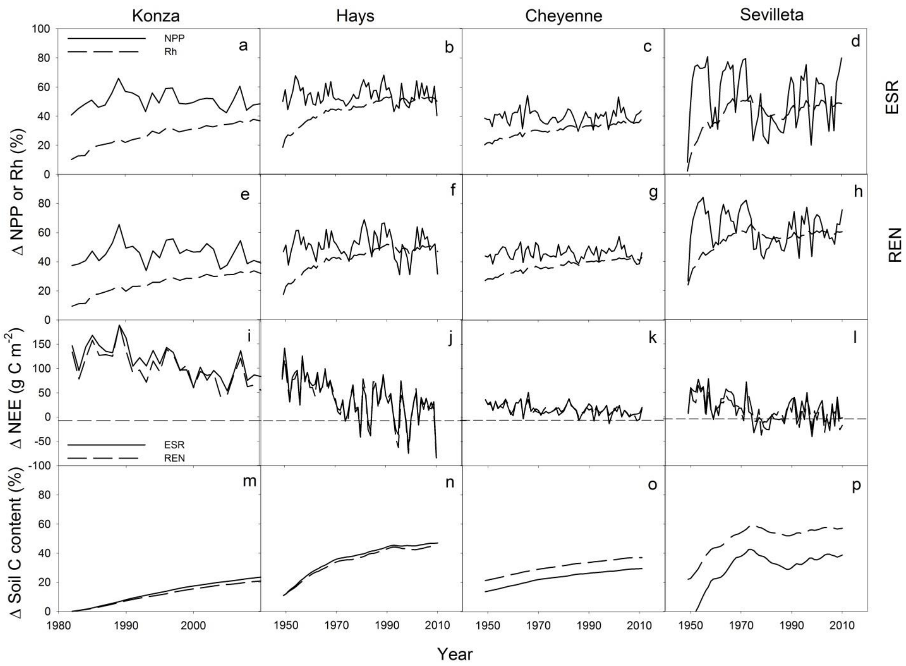

Fig. 3. Drought-induced reductions in net primary production (NPP), heterotrophic respiration (Rh), NEE and soil C content along modeled years in four North American grasslands (Konza: **a, e, i** and **m**; Hays: **b, f, j** and **n**; Cheyenne: **c, g, k** and **o**; Sevilleta: **d, h, l** and **p**). ESR is rainfall event size reduction and REN is reduced rainfall event number. **(a–d)** show reduction in NPP and Rh under ESR. **(e–h)** show reduction in NPP and Rh under REN. **(i–l)** show reduction in NEE and **(m–p)** showed reduction in soil C content.

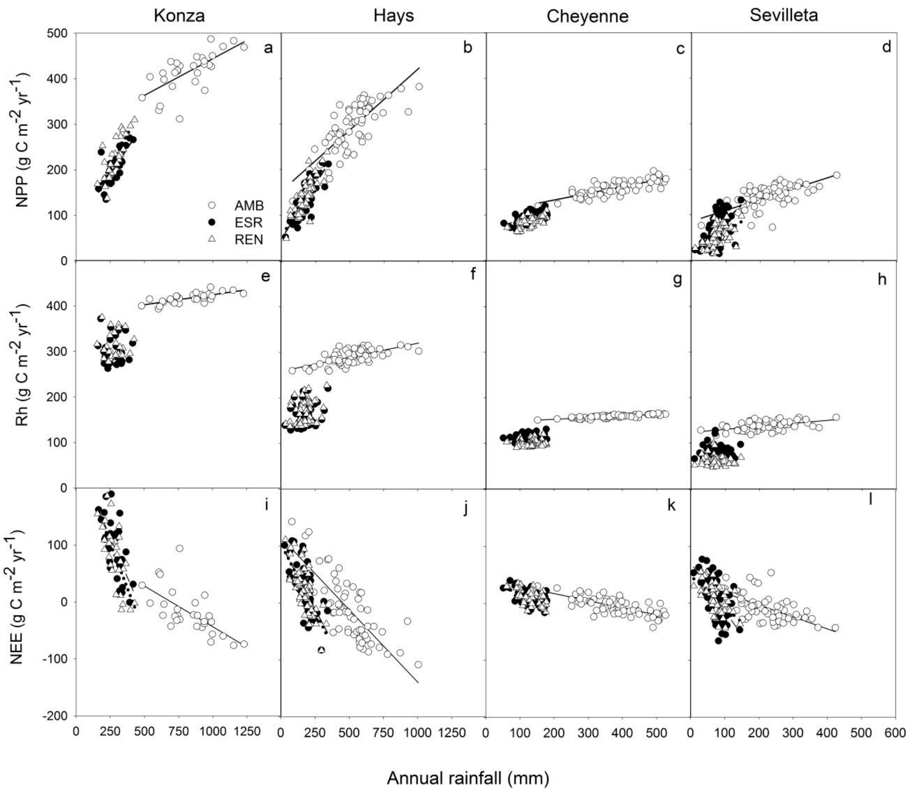

Fig. 4. Relationships between annual precipitation and annual C fluxes under the three rainfall scenarios (AMB: ambient rainfall; ESR: rainfall event size reduction; REN: reduced event number) in four North American grasslands (Konza: **a, e** and **i**; Hays: **b, f** and **j**; Cheyenne: **c, g** and **k**; Sevilleta: **d, h** and **l**). **(a–d)** show relationship between precipitation and NPP. **(e–h)** show relationship between precipitation and Rh. **(i–l)** show relationship between precipitation and NEE.

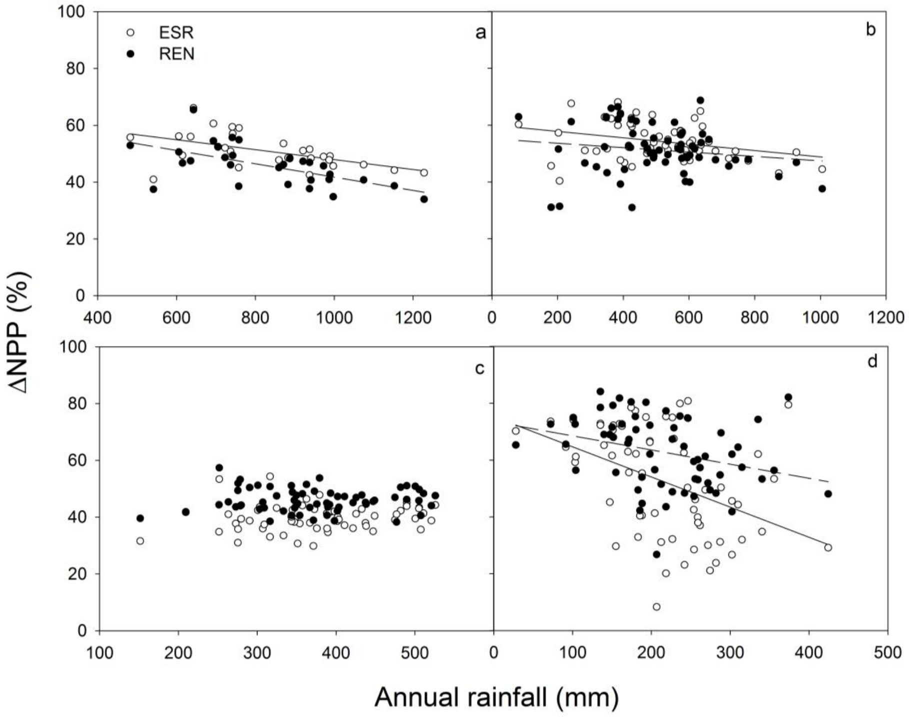

Fig. 5. Relationships between annual precipitation and drought-induced relative reduction (calculated as absolute change caused by drought divided by NPP under the ambient condition) in NPP in four North American grasslands (Konza: **a**; Hays: **b**; Cheyenne: **c**; Sevilleta: **d**). Open circles represent ESR treatment. Solid circles represent REN treatment.

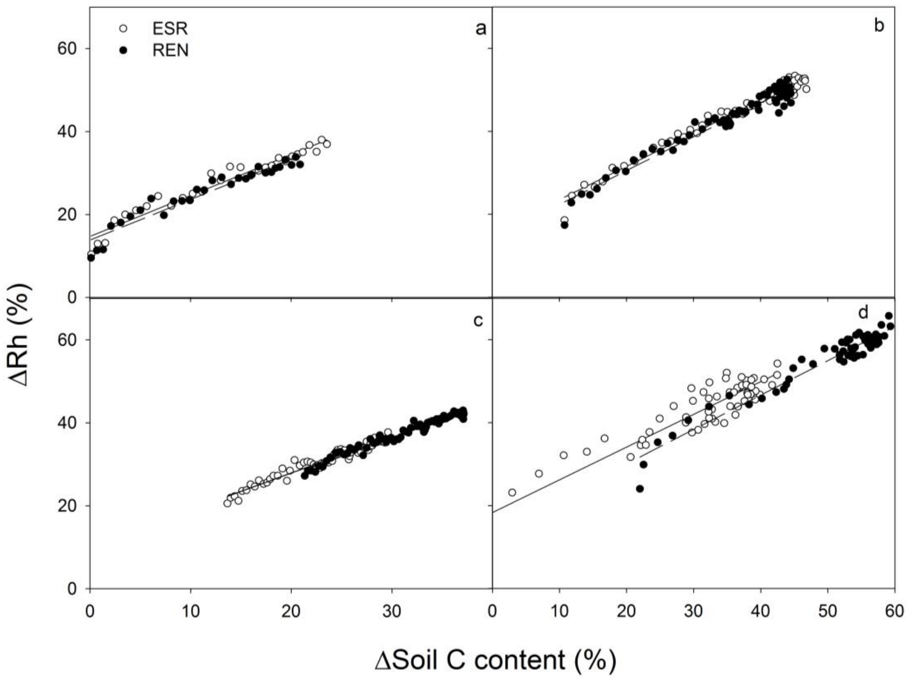

Fig. 6. Relationships between drought-induced relative reduction (calculated as absolute change caused by drought divided by soil C under the ambient condition) in soil C content and relative reduction (calculated as absolute change caused by drought divided by Rh under the ambient condition) in Rh in four North American grasslands (Konza: **a**; Hays: **b**; Cheyenne: **c**; Sevilleta: **d**). Open circles represent ESR treatment. Solid circles represent REN treatment.